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SOME POINTS AND PROBLEMS OF GEOGRAPHICAL DISTRIBUTION.

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I rise to address you to-night, in accordance with the custom—desirable perhaps from your point of view, quite the reverse from mine—which imposes upon your President for the time being the task of delivering an annual disquisition on some branch of malacological science. You will not expect from me, and you will certainly not receive, an address that will bear any comparison with those of my predecessors, in respect either of encyclopædic knowledge or powers of exposition. You must have been well aware, when you placed me in the position which I have the honour to occupy, that my hours of scientific leisure were but few, and that I was of necessity, though not of choice, in respect of the objects of our common worship, "parcus deorum cultor et infrequens."

I propose for your consideration a few points and problems of Geographical Distribution, relating wholly to the Marine Mollusca. My endeavour will be, not so much to solve these problems as to raise them, perhaps to propose difficulties rather than to suggest explanations. One of the soundest ways of learning is, and has been from the time of Socrates till now, by grasping the fact of our own ignorance. And one has little fear that nature will have, even for our children's children, no secrets still to be revealed.

Geographical distribution, if one may so put it, forms a kind of background or setting to the whole study of zoology. The subject of our investigation, whatever it may be, lives its life within a certain definite area or areas of the earth's surface, to the exclusion of the rest—it is 'here' and not 'there'. To state the fact is to invite the demand: Why are certain forms of life found in some localities and other forms in other localities? Modern science answers the question by pointing out a certain correspondence between the organism and its environment, between the circumstances of life and the power to live. When we find an organism living under surroundings, whether of food, light, temperature, soil, etc., which enable it to attain, so far as we can judge, the maximum of its efficiency, and produce descendants equally efficient, we speak of it as enjoying the optimum of environment, and, so long as this optimum of environment is maintained, so long, other things being equal, will the organism continue to live and flourish. On the other hand, if certain of its surroundings become continuously and considerably modified, if, in other words, the environment begins to decline from the optimum, the organism may and probably will be modified also in a manner adverse to its perfect development. And if this process of change in the environment becomes emphasized and prolonged, it may

be that surroundings are produced which are wholly unfavourable to the organism under consideration—in other words, it may be unable to sustain existence any longer.

So far as our present knowledge extends, we are unable to determine, with any approach to demonstration, what amount of modification in surroundings becomes unfavourable to the life of a particular species. Changes apparently insignificant on the one side produce, at times, profound modifications on the other, and it is seldom an easy matter to refer with certainty the production of a definite change in form to its *causa causans*, or, conversely, to predict with accuracy what particular modification of form will result from a known environmental change. For instance, specimens of *Littorina rudis*, Mat., from the coast of Labrador, are habitually much eroded,[1] and our common *L. obtusata*, L., as we follow it northwards in Norway tends more and more to assume the form known as *palliata*, Say; but no precise explanation of these modifications is forthcoming. Conversely, we cannot predict what particular change of form will occur when *Limnæa pereger* is found living in hot water, nor would it be reasonable to assume that all *Limnæa* living in hot springs were similarly modified. One thing is plain, that violent and rapid changes of condition destroy life, while gradual changes are readily tolerated. Even this rule would seem to have its apparent exceptions, for nothing is more striking than to note how certain common littoral marine species begin to die out or become rare on the coasts of South-West Sweden and East Denmark, where the water is not yet brackish. The water of the Kattegat can be but slightly affected by the diminished salinity of the Baltic, and yet we find that such species as *Purpura lapillus*, *Patella vulgata*, *Ostrea edulis*, and all the littoral Trochidæ, which are entirely wanting in the Baltic, are but feebly represented in that broad strait.

Science has long been accustomed to distinguish various areas or zones of distribution, the littoral, the laminarian, the nullipore, or coralline, and the benthal, abyssal, or deep-sea zone, each characterized by its own peculiar groups of Mollusca. Scientific expeditions, from those of the *Lightning* and *Porcupine* in 1868–70, and of the *Challenger* in 1873–6, down to the most recent dredgings of the Prince of Monaco in the *Hirondelle* and *Princesse Alice* in 1912, have established the fact that an increasing number of species are found to live at very distant points on the ocean floor, the uniformity of environment, the absence of sharp breaks in the conditions of life in the great depths, offering only slight barriers to dispersal, and admitting of the widely extended range both of genera and species. Thus *Scaphander punctostriatus* has been found off Spitzbergen, in the West of Ireland, the Azores, and off Culebra Island, West Indies; *Philine aperta* not only in the seas of Norway, the whole of Western Europe, and the Mediterranean, but also off the Canaries, the Cape Verde, the Cape of Good Hope, East Africa, and the Philippines.[2]

[1] K. J. Bush, Proc. U.S. Nat. Mus., vol. vi, pp. 236–47, 1883.
[2] N. Odhner, Kungl. Svensk. Vetensk. Handl., vol. xli (4), pp. 46, 55, 1907.

The *Challenger* dredged *Arca corpulenta* off North-East Australia in 1,400 fathoms, in mid-Pacific in 2,425 fathoms, and near Juan Fernandez in 1,375 fathoms; *Lima goliath* off South Japan in 775 fathoms, and off South Patagonia in 245 fathoms.

It is obvious, however, that our ability to study the vital conditions which govern the existence of the Mollusca, not only in these great depths, but even in comparatively shallow water, is infinitesimal as compared with our opportunities of studying the life conditions of Mollusca which live habitually between or not far below tide-marks. In the one case we can only do a little scraping of the bottom here and there, in the other we have the coastline of all the seas in the world to work upon. It seems possible that in the zeal for deep-sea exploration, which has been prosecuted with such signal success in every branch of marine zoology for more than forty years, we may have lost sight of the rich harvest of knowledge which must assuredly be reaped by a further study of the habits, mode of life, and distribution of the shore fauna, using the term to include the shallow-water fauna as well.

Let me indicate a few problems of distribution which may be said to be waiting for solution.

How does it come about that *Siphonaria*, a littoral genus which occurs in a profusion of individuals wherever it is found, is common throughout the Tropics, and ranges as far south as Cape Horn, the Falklands, St. Paul's Island, and Kerguelen Island, in an area of cold water, whose surface temperature in winter barely exceeds 40° F., and even in summer does not exceed 50° F., while at the same time, in European seas, it only reaches a point on the Spanish coast, somewhere north of Cadiz, where the summer surface temperature is 68° F. and the winter temperature is scarcely less than 60° F.? The same phenomenon is repeated on the south-east coast of North America, where *Siphonaria lineolata*, Orb., reaches its extreme northern range in Georgia, and *S. alternata*, Say, in East Florida and in Bermuda. On the other hand, on the west coast of North America, a species (*S. thersites*, Carp.) is reported from Vancouver and up to 57° N. lat.[1] Is it possible that at the present moment *Siphonaria* is spreading northward along the western shores of Europe and the eastern shores of America? If not, special investigation might throw light on the anomalies of its distribution.

The geographical range of *Patella* forms another subject of interest. It is a remarkable fact that, although many of our own littoral mollusca occur on the eastern and some also on the western coasts of North America, both East and West America, north of the Tropics, are destitute of *Patella* proper altogether. If we may assume that the focus of distribution of a genus is the area, be it great or small, within which the genus attains its largest number of species and its general maximum of development, the foci of the distribution of *Patella* are South Africa, and to a much less considerable extent Southern

[1] P. P. Carpenter, Report, 1863, p. 133 (647); G. W. Taylor, Trans. Roy. Soc. Canada, ser. II, vol. i (4), pp. 17–100, 1895.

Australia and New Zealand. Krauss[1] enumerates no less than twenty-one species of Cape *Patella*, which more modern investigation only reduces to seventeen. *Patella* proper occurs almost all over the world, but is not characteristic of the cold boreal or Antarctic waters. In the latter, as well as in the Californian region, it is largely replaced by the *Nacella* group, while in North Europe and the north-east coast of Asia it becomes rare in species. Our own *Patella vulgata*, L., finds its northern limit in the Faroe and Lofoden Islands; it does not occur in Iceland or in Greenland, and thus took no part in the spread of those littoral Mollusca which are conveniently described as 'circumpolar'. The *Helcioniscus* group of *Patella* spreads all over the Eastern Hemisphere and touches the Western at Chili, Juan Fernandez, and the Sandwich Islands, but is absent from West Africa, where *Patella* proper is strongly represented. On the western shores of North and South America *Patella* is replaced by *Acmæa*, except within the Tropics, where a few species of true *Patella* occur, amongst them the giant *P. mexicana*, Brod., ranging from Mazatlan and Acapulco to Paita, and occasionally measuring 14 inches in length. The fact is significant that *Acmæa* is entirely absent from all African waters, where *Patella* is so abundant, while it occurs liberally in certain districts, i.e. Western North America, from which *Patella* proper is absent. Yet it would not be safe to assume that the genera are mutually exclusive, or that shores not occupied by the one genus have been appropriated by the other. Further study of their distribution would probably throw light on these points. The scarcity of Patellidæ on the coast of East America may perhaps be due to the want of rocky surface to which they could attach themselves, the coast being, in the main, low-lying and sandy.

Haliotis is another genus, belonging in the main to shallow water, whose distribution would repay further investigation. Certain facts are plain: that Australia and the adjoining seas are the focus of its distribution, and that there are two well-marked sub-foci in Japan and North-West America. "Not one species[2] is found on the eastern coast of North or South America, and only one (*H. pourtalesii*[3]) on the west coast of America south of Lower California." The northern range of our own *H. tuberculata* is, as is well known, the Channel Islands, 49° N. lat. It would be interesting to know exactly how far north *H. kamschatkana*, Jonas, extends on the coasts of British Columbia and Kamschatka. Nothing definite seems to be known of the range of the South African species on the east and west coasts of that continent.

The distribution of *Purpura*, a very marked littoral genus, would amply repay careful study. Especially one would like to know the

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[1] *Südafrikanischen Mollusken*, pp. 43–57.

[2] H. A. Pilsbry, Manual of Conchology, vol. xii, p. 73.

[3] Dredged in 33 f. sand, at Charles I., Galapagos. Pourtalés dredged one living *Haliotis* (the specimen has since been lost) from the bed of the Gulf Stream, in 200 f., near Florida reefs. No specimens of *Haliotis* have since been found in the West Atlantic or Gulf of Mexico.

extreme north and south limits of our own *P. lapillus*, L., no less in Europe and Africa than on both sides of North America and in Japan, and whether Adanson was right or wrong when he enumerated it among the Mollusca of Senegal.[1]

Purpura hæmastoma, L., has long been known to inhabit both sides of the tropical Atlantic, from West Africa, the Mediterranean, and the coasts of Portugal and France on the one hand, to Brazil, the West Indies, and the southern states of Eastern North America on the other. But it is only of recent years that we have learned that *P. coronata*, Lam., has crossed the Atlantic too, and has appeared in Demerara[2] and Trinidad and in East Guatemala.[3] The West Indies have retaliated by sending to West Africa a form (*P. eudeli*, Sow.) whose relationship to *P. patula*, L., is so close as to leave no doubt of its origin, and scarcely any that it should be counted as a mere variety.[4] Has this process of exchange between the shores of the Atlantic at its narrowest part, over 1,600 miles, gone any further, e.g. in any form of *Littorina* possessing a free-swimming larva? The transit of the larval form from one coast to another would be facilitated by the remarkably equable temperature of the intervening water (a steady 77°–80° F. all the year round), by the absence of any strong north or south current, and by the more or less circulatory drift of water between the two continents.

If larval forms of *Purpura* can pass from West Africa to South America, and vice versa, it is easy to understand how *P. columellaris*, Lam., an obvious derivative of *P. patula*, L., became established at the Galapagos, only 600 miles from the nearest mainland. The heated water of the Bay of Panama follows the coast southward until it reaches Cape San Lorenzo, in lat. 1° S., where it is deflected westward, straight for the islands. Trees from the mainland, with the leaves still upon them, have been found cast up on the island shores. The molluscan fauna of the Galapagos thus exhibits large contributions from the Panamic and Peruvian regions, with a very slight admixture of the Indo-Pacific element.[5]

Again, *P. neritoidea*, L., is a common West African littoral shell. It is also found in the Cape Verde, 300 miles from the coast, and, as a variety scarcely distinguishable from the type, on Ascension Island, nearly 900 miles from the nearest African land.

Further research on the relationships of adjacent groups of *Purpura* would probably bring out valuable results, for the genus is almost worldwide and abundant in species and in individuals. Some light might be thrown on the remarkable way in which it is replaced, on the coasts of Chili and of the Magellanic and part of the Patagonian

[1] M. Adanson, Hist. nat. Sénegal: Coquillages; Paris, 1757, pp. 106–7, pl. vii, fig. 4.
[2] A. H. Cooke, Journ. Malac., vol. iv, p. 69, 1895.
[3] H. A. Pilsbry, Nautilus, vol. xiii, p. 130, 1900.
[4] The species was described by Sowerby in Journ. Conch., vol. x, p. 74, 1903.
[5] These facts are due to W. H. Dall, Report on a Collection of Shells from Peru, etc.: Smiths. Inst. Proc. U.S. Nat. Mus., vol. xxxvii, pp. 147–294, 1909.

province, by the singular toothed *Acanthina* (*Calcar*) and by *Concholepas*, both of which genera appear to have a wide but as yet undetermined range on the coasts of West America.

Similar attention might be paid to *Nerita* and also to *Littorina*, due regard being had to the fact[1] that, in the latter case, some species which live in the neighbourhood of high-water mark are viviparous, while others, which live at a lower tide-level, produce a trochosphere or veliger embryo. The exact distribution and economic habits of such widely spread species as *mauritiana*, Lam., *aspera*, Phil., the group which centres round *scabra*, L., *miliaris*, Quoy, and *malaccana*, Phil., would repay investigation and might bring out some interesting facts.

We still continue to speak of the distribution of marine Mollusca under the headings of 'districts' or 'provinces' or 'regions', or whatever name we choose to employ, and indicate the fact that certain wide areas or stretches of adjacent coast-land are characterized by the occurrence of certain genera and species, as contrasted with the phenomena observed in the case of other geographical areas. This method of subdivision is convenient, but it needs careful handling. The results of deep-sea dredging during the past few decades have accentuated the fact that these subdivisions apply solely to the Mollusca of the shore or of shallow water. And we must be careful to recollect that in scarcely any instance is it possible to draw a hard and fast line between one 'region' and another. On the contrary, adjacent regions seldom fail to overlap. On the west coast of America, for instance, the Magellanic region overlaps the Peruvian, and the Peruvian the Panamic, and the same is the case with the regions further north, the Californian and the Aleutian, while the Aleutian in its turn graduates into the north circumpolar region. All that we can allow ourselves to mean, when speaking of the limits of a region, is that at a certain point on the map we are able to say that the characteristic fauna of that region occurs infrequently, or is beginning to be sensibly replaced by a fauna characteristic of another region.

Some regions, owing to special geographical facts, may be more sharply defined than others, at one or at both extremes. If we were asked to cite the sharpest break in existence between one marine fauna and another we should lay our finger on Cape Hatteras, at which point a vast number of prominent tropical species find their northern limit. But how can we name a point of separation between, say, the Californian and Panamic, or between the Panamic and Peruvian regions? The main but not the only factor in determining the limits of a region is the surface temperature of the sea-water, as distributed by ocean currents.

The truth is that the present state of our knowledge, as regards the geographical limits of this or that fauna, is singularly defective. Large portions of coastline remain at present unexplored, and it is

[1] W. M. Tattersall, quoted by B. B. Woodward in Proc. Malac. Soc., vol. viii, p. 282, 1909.

only necessary to point to the map of Africa, from Morocco and the mouth of the Orange River, and from Lorenzo Marques to Cape Guardafui, or to the coast of China from the mouth of the Mekong to Korea, to show that at present our knowledge is limited to the species which have been collected at a few isolated spots, while no systematic exploration worth the name has as yet taken place. One is not without the hope that before long expeditions will be equipped with the sole object of exploring the fauna of *certain definite pieces of coastline*, more particularly those where geographical and faunistic regions, as at present understood, tend to merge into one another—the marchlands of adjacent kingdoms.

P. Fischer defines[1] the Lusitanian region as comprising the Atlantic coasts of France, Spain, and Portugal, the Mediterranean, the North-West African coast from Tangier to Cape Juby, and the Azores, Madeira, and Canary groups. Paul Pallary, after remarking[2] that recent researches tend to show that even the Mediterranean fauna is not yet completely known, continues as follows: "Si donc la faune d'une mer entourée de pays civilisés et d'une étendre relativement restreinte est encore incomplètement étudiée, quoi de surprenant que nous ne sachions que bien peu de chose sur celle des côtes occidentales de l'Afrique?" And he goes on to say that he found, between Cape Spartel and Mogador, *Patella compressa*, three species of *Vetus*, four of *Marginella*, including *glabella*, *monilis*, and *cornea*, and a *Pusionella*, all species characteristic of the Senegalian fauna, and never before recorded from so high a latitude. Already in the Canaries a considerable proportion of equatorial species occur, and he thinks that the tropical fauna comes up very high on the west coast of Africa, even reaching the Algerian coast, so that the limits of the old Lusitanian province or region must be modified and made to lie much further north, at least as far as the Straits of Gibraltar. And when one adds that the proposal implies the addition of at least 800 miles of coastline to the Senegalian region, it is quite clear that further exploration of obscure and remote coast-lands promises to provide us with plenty of material for discussion.

Conversely, M. Ph. Dautzenberg, remarking[3] on the molluscan fauna of the inhospitable coast between the bay of Lévrier and Sénegal (N. lat. 21°–16°), says that the proportion of 'Mediterranean' species which spread along the western coast of Africa is greater than has been supposed. Thus, in the collection under review, of ninety-eight Mediterranean species which occur, fifty-eight live in the Cape Blanco seas and thirty-four on the coasts of Mauretania and Senegal.

The problems involved are not of a simple nature, and may be complicated by all manner of interferences on Nature's side. As an

[1] Man. de Conch., p. 143.

[2] Bull. Sci. France Belgique, vol. xli, pp. 421–5, 1907.

[3] "Sur les Mollusques marins provenant des campagnes scientifiques de M. A. Gruvel en Afrique occidentale, 1906–9": Comp. Rend. Acad. Sci., vol. cxlix, pp. 745–6, 1909.

example of a district on which we are remarkably destitute of information we may take the whole South American coastline from Venezuela to Buenos Aires, and even further south. What little we know inclines us to believe that the Mollusca of these thousands of miles of coast is typically Antillean in character; at any rate *Purpura hæmastoma*, L., both typical and in varieties, is found as far south as Rio Grande do Sul (32° S.) and the mouth of the Rio de la Plata. That many thoroughly littoral species should be able to cross the present volume of the discharge of Amazonian fresh-water, covering some hundreds of square miles, seems so incredible that it may be held that the existing coast fauna antedates the existence of that and other streams, at least in their present immensity.[1]

Verrill has pointed out[2] that the entrance of Long Sound and the bays and sounds lying south of South Massachusetts are inhabited by two separate molluscan faunas, the shallower waters of the bays being occupied chiefly by southern forms belonging to what he then calls the Virginian fauna, while the deeper channels of the central parts of the sound are inhabited exclusively by a northern fauna. The cause of this apparently anomalous state of things is that an offshoot of the cold Arctic current which sweeps round Nova Scotia sets into the middle of the sound and produces, both at the surface and at the bottom, a change of temperature, which, within a space of only 2 miles, amounts to as much as 5° F. Thus the littoral fauna is of a comparatively southern type, while even the shallow-water fauna, at depths of no more than 18 to 39 fathoms, is strictly northern, consisting of the following amongst other species: *Molgula pilularis*, *Glandula mollis*, *Cardita borealis*, *C. novangliæ*, *Yoldia sapotilla*, *Y. limatula*, *Nucula proxima*, *Astarte quadrans*, *A. castanea*, *Modiolaria nigra*, *M. corrugata*, *Chrysodomus pygmæa*, *Margarita obscura*, *Cylichna alba*, and many others.

Much useful aid in exploration may be gained from geology in showing that certain modifications of climate and of elevation, otherwise unsuspected, must have taken place. Thus, to take one instance out of many, G. Bardason has shown,[3] from the evidence of Pleistocene marine beds in North Iceland, that within comparatively recent times the sea was at least 4 metres above its present level, with the effect that the temperature of that particular region must have been higher than it is at the present epoch, or much as it is now in South-West Iceland. This is shown by the presence in the deposits of *Purpura lapillus* and *Zirphæa crispata*, and by the absence of *Pecten islandicus*. As the sea retreats the temperature, in northern regions, becomes lower, and the conditions assume a more Arctic character.

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[1] W. H. Dall, "Additional Notes from the Coast of Southern Brazil": Nautilus, vol. vi, pp. 109–12, 1893. "List of Shells collected at Bahia, Brazil, by Dr. H. von Ihering": ibid., vol. x, pp. 121–3, 1897.

[2] Ann. Mag. Nat. Hist., ser. iv, vol. ix, pp. 92–7, 1872.

[3] "Maerker efter Klima- og Niveanforandringer ved Húnaflói i Nord-Island": Vid. Medd. Copenhagen, 1910 (ii), pp. 35–79.

Again, certain northern species which are littoral under normal conditions of life tend to seek deeper water as they move southward, while exactly the reverse is the case with certain southern species, which are found in shallower water in northern than in southern latitudes.[1] This seems to emphasize the point that temperature is of prime importance in determining habitat, northern species finding the cold they are accustomed to by migrating to somewhat deeper water in the south, and southern deepish water species finding the low temperature they need in shallower water as they move north. Mediterranean species of the coralline and abyssal fauna are found to live, as a rule, in depths less profound than they do in the Atlantic. *Buccinum undatum*, L., which is common at low-water mark at certain places in Northern and Eastern England, is never found between tide-marks at Scilly. *Neptunea antiqua*, L., may be found alive on the shores of Shetland, but in Southern and Western England it retires into deeper water. *Emarginula crassa*, J. Sow., is not rare on the shore at Oban; in the Gulf of Gascony it has only been dredged at 400–500 metres.

It must not be forgotten that conditions of life in every quarter of the globe can never be regarded as absolutely permanent. Changes of environment, some vast and sweeping, others apparently trivial and scarcely detected, are in operation and must affect, to a greater or less degree, the life of the organisms which inhabit the different areas. Collectors who work a particular ground are familiar with the fact that certain species may be found by the score or by the hundred in a given locality, and then for years they will be extremely scarce, and then will reappear again, as numerous as before. Of *Aplysia depilans*, L., "a small fleet arrived in Torbay in 1875 and lingered for a couple of years . . . previous to that only one specimen had been found there." Of *Oscanius membranaceus*, Mont., "in 1874 a large fleet appeared simultaneously at Weymouth and at Torbay, and again in the latter district in 1877 and 1887."[2] "At one time *Nassa fossata*, Gld., at another *Periploma discus*, Stearns, at another *Lima orientalis*, Cpr., or *Scalatella striata*, Cpr., are found by the dozen in San Pedro Bay [Cal.], and then for years after only a few are found at a time."[3] It must be remembered too that certain Mollusca, notably the Opisthobranchia and Nudibranchia, come ashore in the breeding season to deposit their eggs and then retire to deep water.

Occasionally we are able to observe a definite extension of area on the part of a species, without being able to assign any definite cause. When Jeffreys wrote his *British Conchology* (1865 is the date of vol. iii) *Acmæa testudinalis*, Müll., had not been observed on our eastern coast south of Hartlepool; in 1890 it had reached Scarborough, in 1910 it was south of Bridlington, and is said to be extending its range rapidly

[1] See W. H. Dall, Bull. U.S. Nat. Mus., vol. xxxvii, pp. 1–221, 1889.
[2] J. T. Marshall, Journ. Conch., vol. xiv. pp. 65, 66, 1913.
[3] S. P. Monks, Nautilus, vol. vii, p. 75, 1893.

still further south.[1] Has anyone observed that the surface temperature of the water on our north-eastern coast has fallen, during the last fifty years? *Cassidaria tyrrhena*, L., which was first added to the British fauna in 1870, and subsequently dredged off the Kerry coast and off the Scillies, has of late been trawled in considerable numbers in the deep trough between Milford Haven and the Irish coast, off the Saltees lightship, and appears to be moving northward.

In the list of the Mollusca of Long Island[2] published by Sanderson Smith and Temple Prime in 1870, a list which embodied the results of eleven years' collecting, *Littorina littorea*, L., did not occur. F. N. Balch, publishing[3] in 1899 a list of the marine Mollusca of Coldspring Harbour, Long Island, remarks: "Ten years ago it might have been possible to define a spot within 60 miles by saying it was a place where *Purpura lapillus* was not, and *Litt. littorea* was, found, but now the wave of the conquering European species has spread far down toward Virginia, and at Coldspring the native competitor (*Nassa obsoleta*) begins to yield room."

When the agency of man gives them a chance of extending their area the Mollusca are as quick to take advantage of their opportunity as the rabbit was in Australia. The spread of Mediterranean and Red Sea species into the waters of the Suez Canal has been commented upon by Tillier and Bavay, by Faurot and others. No doubt our American friends will be equally ready to note the results of the opening of the Panama Canal, and to observe whether the 'homologous species' which, in some numbers, inhabit the two sides of Central America, show any signs of approximation, as a result of the mingling of waters which have been separated since the Miocene epoch.

We have watched the almost meteoric swiftness with which *Petricola pholadiformis*, Lam., and *Crepidula fornicata*, Lam., have established themselves in European waters. The former, after having first been noticed in the River Crouch, Essex, in 1890, was at Shellness and Herne Bay in 1896, in 1901 it had reached Belgium, and was notified from Ostend in 1903 and Dunkirk in 1906, in 1907 it had spread all over the Suffolk coast, Denmark notified it in 1906–7, in 1908 it was at Noordwijk, Holland, in 1910 at the mouth of the Medway, and the same year at Shallinger, Denmark. It will be interesting to see at what point short of the Baltic it stops. Of *C. fornicata*, dead shells of which were first notified at Cleethorpes in 1887, 10 tons of live specimens were dredged[4] in four weeks in the Blackwater River twenty years later.

Urosalpinx cinerea, Say, has been transplanted with East American oysters to the Pacific coast. A quart of specimens of this oyster scourge has been collected in less than ten minutes at Belmont, near San Francisco.[5]

[1] J. A. Hargreaves, Journ. Conch., vol. xiii, p. 89, 1910.
[2] Ann. Lyc. Nat. Hist. N. York, vol. x, pp. 377–407, 1870.
[3] Proc. Boston Soc. Nat. Hist. (7), vol. xxix, pp. 133–62, 1899.
[4] J. Murie, Zoologist, ser. IV, vol. xv, pp. 401–15, 1911.
[5] R. E. C. Stearns, Nautilus, vol. viii, p. 13, 1894.

The best-studied coastline in the world is, beyond a doubt, that of Eastern North America, from Texas and Florida to Labrador, thanks to the work of Dall, of Verrill, Bush, and many others. Let us for a moment employ some of the material gathered by them,[1] and fix our attention on the tropical fauna of the extreme south-east States, a fauna which is in close alliance with the West Indian. What is the extreme northern range along that coast of such thoroughly tropical genera as *Conus*, *Cypræa*, *Trivia*, *Strombus*, *Oliva*, *Olivella*, *Fasciolaria*, and the *Phyllonotus* group of *Murex*?

Of *Conus* ten species occur, nine of them on Florida Keys; four reach Cape Hatteras, none further north.

Of *Cypræa* there are three species, all West Indian; one only (*C. exanthema*, L.) reaches Cape Hatteras, and no further.

Of *Trivia* there are seven species, all found on Florida Keys, but only one reaches Cape Hatteras, and no further.

Strombus is represented by five species (four of them West Indian); all five occur on Florida Keys; three only reach East Florida, one reaches Georgia, one (*pugilis*, L.) Cape Hatteras, and no further north.

Oliva has two species; one of these reaches Cape Hatteras, and no further.

Olivella has six species, all West Indian; three reach Cape Hatteras, but no further north.

Of *Fasciolaria* there are three species, all represented on Florida Keys; all reach Cape Hatteras, but no further.

Finally, of *Phyllonotus* there are four species; two of these reach Cape Hatteras, but no further.

This list might be considerably extended, and it would not be easy to find a more striking instance of the power of a current of warm surface-water to carry a tropical fauna northward. Cape Hatteras, be it remembered, is in about the latitude of the Straits of Gibraltar. The Gulf Stream, issuing from the Gulf of Mexico, makes a right-angled turn at Cape Sable, the extreme southern point of Florida, and hugs the East American coast more or less closely until it reaches Cape Hatteras, when it parts company with the land and moves north-east and east across mid-Atlantic. A further factor which accentuates the sudden break in the range of the tropical fauna, and makes the northward barrier more effective, is the fact that a cold current, the remains of the Polar and Labrador drift, running a westerly and southerly course from the outer banks of Newfoundland[2] and the south coast of Nova Scotia, parallel to, but in the reverse direction to, the Gulf Stream, impinges on the North American coast

[1] See particularly W. H. Dall, "A preliminary Catalogue of the Shell-bearing Marine Mollusca . . . of the south-east coast of the United States": Bull. U.S. Nat. Mus., vol. xxxvii, pp. 1–221, 1889.

[2] "The Grand Banks of Newfoundland . . . are inhabited by an extremely Arctic fauna, including many species of Mollusca which have not yet been found further south" (A. E. Verrill, Trans. Connect. Acad., vol. v, pp. 447–587, 1878–82).

somewhere just north of where the Gulf Stream leaves it, and thus brings a cold-water fauna down to a point in the latitude of Lisbon, and effectually prevents the tropical fauna from creeping any further north. Thus *Acmæa testudinalis*, Müll. (a cold-water species), ranges as far south as New Jersey, in N. lat. 40°, while on the European side it has not been found south of about 54° on the east coast of England, and about 53° on the Irish coast, while hardy circumpolar species like *Macoma balthica*, L., *Mya arenaria*, L., and *Mytilus edulis*, L., creep as far south as Hatteras and even Georgia.

It is interesting to observe that besides the migrants from the sub-Arctic fauna southward, and from the tropical fauna northward, the eastern shores of North America have a temperate fauna of their own, which appears to be comparatively unaffected by the great change of temperature which occurs at Cape Hatteras. For we find a large number of species, corresponding to the temperate element in our own seas, which occur commonly between Cape Cod and Georgia or even Florida. Possibly this fauna may be considered to have taken up its abode on these coasts before the present conditions of current became fixed. Thus there are five species of *Fulgur*, all of which occur in Georgia, which may be regarded as their metropolis; three of these reach the West Indies and three Cape Hatteras, but two range northward as far as Cape Cod. *Nassa trivittata*, Say, extends from St. Augustine in North Florida to Nova Scotia, *N. vibex*, Say, from Aspinwall to Cape Cod, *N. obsoleta*, Say, from Tampa to Nova Scotia. Two muricidan species, both strongly characteristic of East American temperate shores, are *Urosalpinx cinerea*, Say, and *Eupleura caudata*, Say. The former ranges from Florida to Nova Scotia, the latter from Florida to Cape Cod. Similarly, *Astyris lunata*, Say, ranges from Turtle Harbour in West Florida to Cape Ann, and *Anachis avara*, Say, from Florida Keys to Massachusetts Bay. In all these cases what may be called the indigenous fauna pass with ease a barrier which proves so formidable to the northern and southern migrants.

Now let us compare the position on the western side of North America. Our information may not be quite so full, but the general trend of distribution is plain. Here the tropical fauna of the Panamic region, instead of being carried far northward along the coast by a warm-water current, is checked by the far-reaching effect of a stream of cold water. The Kuro Shio current, issuing from the warm seas to the south of Japan, and crossing the North Pacific, loses much of its warmth in the passage, and is very possibly reinforced by cold water from the north. It impinges on the West American coast about the latitude of Queen Charlotte Island (N. lat. 52°), and breaks into two branches, the northern of which washes the coasts of North Canada and Alaska, while the southern moves southward along the coasts of Oregon and California. The effect of this cool current sweeping southward must obviously be to keep back the northward spread of the tropical species. The result is that the same genera, *Strombus*, *Oliva*, *Cassis*, *Conus*, etc., which were well represented up

to lat. 36° N. on the eastern side, are far less numerous at the same latitude on the western. Santa Barbara, in 35·5° N. lat., shows few traces of a tropical fauna. The surface temperature of the sea-water at Cape Hatteras in August is 77° F., in February 68° F. (mean 72½° F.); the corresponding temperatures at Sta. Barbara are 66° F. and 59° F. (mean 62½° F.); in other words, the February temperature on the east coast exceeds the August temperature on the west on the same parallel.

These special conditions enable the temperate fauna of Upper California to penetrate far southward; *Priene oregonensis*, Redf., e.g., has been found at Monterey, several of the *Chlorostoma* group at Margarita Bay, in lat. 24° N., *Purpura ostrina*, Gld., at the same place. Closer investigation of the fauna of Lower California is much to be desired, but one interesting fact is plain, that the great Gulf of California, nearly 900 miles in length, forms a great hot-water basin and is quite unaffected by the ocean currents. The result is that it bears a tropical fauna up to its extreme northern point, so that the Californian peninsula, more particularly in its northern portion, has a tropical fauna on its eastern side, and a mixed tropical and sub-tropical fauna on its western, and at certain points these two fauna are within 50 to 60 miles of one another across the isthmus. The mean annual surface temperature of the water inside the gulf is somewhere near 80° F., on the outside it is about 72° F.

It may be remarked parenthetically that the Red Sea and the Persian Gulf offer similar examples of enclosed seas whose surface temperature is very high. That of the lower portion of the Red Sea rises to 90° F. in the summer, and that of the Persian Gulf to the astonishing figure of 95° F. The heat of the Red Sea explains why at Suez we have tropical forms such as *Pyrula*, *Strombus*, *Murex* (typical), and *Nerita* living on the shore, in a latitude well to the north of the Canaries. The head of the Persian Gulf is in exactly the same latitude as Suez.

Now to come a little nearer home. On the eastern shores of the Atlantic many southern species enjoy a wide range northward, and many northern species an equally wide range southward. This is due to the extremely equable temperature of the surface-water of the sea from Norway to Morocco. Along this vast stretch of coast there is no pronounced equatorial current moving northwards to bar back the northern species, still less is there any polar current sweeping southward along the coast to check the spread of the southern species. It is quite true that the Gulf Stream and Antillean Current exercise a powerful influence upon the temperature of our northern waters, but that influence is so widely diffused, and the changes it induces are so gradual, that at no point is there any *sudden* variation in temperature, such as is found on the western side of the Atlantic. Even the south-western shores of Nova Zembla (N. lat. 72°) are washed in August by water no colder than 40° F.

The isothermal line of 50° in August all but touches the North Cape; the isotherm of 60° in the same month is not reached till south of the Wash, on the east of England, and Lough Swilly, to

the west. Southward of these points the temperature of the surface-water continues singularly equable, for the August isotherm of 70° F. is not reached till Cadiz, and that of 77° F. not till N. lat. 20°, far to the south of the Tropic. And the February surface temperatures are equally striking. Water from 40°–49° F. tempers the Norwegian coasts as far north as the Arctic Circle, and encloses the whole of the British Isles and the French coast as far south as La Rochelle. Here begins the isotherm of 50° F., coming down from a point off North-West Ireland; water at 60° F. is not reached on the Portuguese coast till Lisbon, and the isotherm of 68° F. is attained near the latitude of the Cape Verde, well to the south of lat. 20° N.

These singularly equable conditions of surface temperature seem to explain many of the prominent features of the distribution of the shallow-water and shore Mollusca of Western Europe. We can understand, on the one hand, how it is that Finmark and the Mourmane coast have a rich littoral fauna,[1] that warm-water genera such as *Pinna* and *Meretrix*, *Ovula* and *Truncatella*, *Phasianella*, *Triforis*, *Ocinebra*, *Haliotis*, and *Lotorium* reach our own coasts. And we can also understand how northern species have penetrated southward; how, for instance, *Buccinum undatum*, L., and *Neptunea antiqua*, L., reach South-Western France, how *Littorina littorea*, L., reaches the Straits of Gibraltar, *L. obtusata*, L., the Western Mediterranean, and *Purpura lapillus*, L., Algarve and even Mogador. R. T. Lowe remarks[2] that of a collection of marine Mollusca picked up on the shore at Mogador, close upon three-fifths are found commonly in Britain. R. McAndrew, dredging in 35–40 fathoms off Mogador, obtained 22 species of shells, 16 of which were British; and of 125 species obtained by him at Madeira, 58 are common to our own shores.[3]

I should like to see the distribution of the marine Mollusca of Western Europe, both in its northern and southern extension, and in range of depth, worked out with the same precision and accuracy as has been done in the case of the Mollusca of the eastern coast of North America. At present there is plenty of enthusiasm, but little organization, plenty of statistics, but no centralized store-room for their preservation. Britain, in virtue of its central position, looking as it does both north and south, and possessing an enormous stretch of coast-land, should take the lead, and I can think of no body better fitted to undertake the task of collecting material, sifting evidence, formulating tables of statistics, and keeping them up to date, and generally of acting as a depository of facts and an authoritative court of reference, before which all questions bearing on the subject ought to be brought, than the Society which I am now addressing. The task would be serious; it ought not to be beyond our powers.

The British marine molluscan fauna—leaving out of consideration such abyssal species as may be reckoned in the list—is clearly made

[1] S. Herzenstein, Congrès intern. Zool., vol. ii, pt. ii, pp. 127–47.
[2] Journ. Linn. Soc., Zool., vol. v, pp. 169–204, 1861.
[3] Ann. Mag. Nat. Hist., ser. II, vol. x, pp. 100–8, 1852.

up of three elements: (1) a northern element, consisting of species which may be supposed to have spread southwards from Arctic or sub-Arctic latitudes; (2) a southern element, consisting of species which have spread in the reverse direction from more southern latitudes; (3) an element which is probably indigenous in our own and neighbouring temperate seas.

Perhaps the most striking way of bringing out this point is to instance particular genera which happen to include species of both northern and southern origin. Of *Littorina*, for instance, we have four species on our shores, three of which are northern and one southern in origin: *littorea*, L., a northern form, ranges from the White Sea and Mourmane coast to Lisbon and the Straits of Gibraltar; *rudis*, Mat., from the Glacial Ocean to Southern Spain[1]; *obtusata*, L., extends from the White Sea, Finmark, and Iceland to South Spain and South France, but not further east in the Mediterranean. All these three species are found on the east coast of North America. *L. neritoides*, L., on the other hand, is a markedly southern species, ranging from the Canaries and Madeira to North Britain. Of *Acmæa* we have two species, one of markedly southern, the other of equally clear northern origin; *A. virginea*, Müll., ranges from St. Helena, the Azores, and Madeira to North Norway; *A. testudinalis*, Müll. (a thoroughly Arctic form), occurs from Nova Zembla, North Labrador, Greenland, and all Arctic seas to the Yorkshire coast on this side of the Atlantic, and to New Jersey on the other. *Emarginula* is represented by three species, each of which appears to belong to a different fauna; *E. crassa*, J. Sow., is a northern form, curiously, as it seems, absent from the eastern coasts of Britain, and found in littoral and shallow waters no further south than Dublin Bay; *E. fissura* (L.), with a range from Finmark to the Canaries, seems characteristic of the temperate fauna, while *E. conica*, Schum., is a strictly southern form, ranging from the Mediterranean and South Spain to the Dorset coast, but no further north. The same point may be illustrated in other of the genera occurring on our shores, e.g. *Modiolaria*, *Crenella*, *Rissoa*, *Scala*, *Calliostoma*, and *Lunatia*, of which latter genus *pallida*, Brod., *montagui*, Forbes, and *affinis*, Gmel., are northern forms, *alderi*, Forbes, belongs to the temperate fauna, while *catena* (da Costa) and *sordida*, Phil., are of southern origin.

The following members of the British marine fauna rank as 'northern' species (the list has no pretensions to completeness, and Nudibranchia and Cephalopoda are not included):—

*†‡§*Tonicella marmorea* (Fabr.).[2]
†*T. rubra* (Lowe).
*†*Craspedochilus albus* (L.).
*†‡*Nuculana tenuis* (Phil.).
**Limopsis aurita* (Broc.).
†‡§*Modiolus modiolus* (L.).

[1] Unless we unite *rudis*, Mat., and *saxatilis*, Oliv., in which case the range extends all over the Mediterranean, Adriatic, and Black Seas.

[2] R. McAndrew is said to have dredged this species at Carthagena in 5–10 f., which seems improbable.

*†‡*Modiolaria discrepans* (Leach).
*†‡*Crenella decussata* (Mont.).
**Lima elliptica*, Jeff.
†‡*L. subauriculata* (Mont.).
**Limea sarsii* (Lov.).
*†*Astarte compressa* (Mont.).
†*Arctica islandica* (L.).
**Cryptodon croulinensis* (Jeff.).
**Cuspidaria abbreviata* (Forb.).
**Dentalium striolatum*, Stimps.
**D. agile*, M. Sars.
*†*Acmæa testudinalis* (Müll.).
*†‡*Lepeta cæca* (Müll.).
L. fulva (Müll.).
*†*Puncturella noachina* (L.).
‡*Emarginula crassa*, J. Sow.
**Propilidium ancyloide*, Forb.
Rissoa albella, Lov.
†*Onoba striata* (J. Ad.).
†*Skenea planorbis* (Fabr.).
*†‡*Lunatia pallida* (Brod. & Sow.).
L. montagui (Forb.).
*†*Amauropsis islandica* (Gmel.).
†‡*Velutina lævigata* (Penn.).
*†§*V. flexilis* (Mont.).
**Scala grœnlandica* (Chem.).
Cœcum imperforatum (G. Ad.).
**Trichotropis borealis*, Brod. & Sow.
†*Buccinum undatum*, L.
B. humphreysianum, Benn.
Liomesus dalei (J. Sow.).
*†§*Volutopsis norvegica* (Chem.).
**Beringius turtoni* (Bean).
†*Tritonofusus islandicus* (Chem.).
T. gracilis (da Costa).
**T. propinquus* (Ald.).
T. fusiformis (Brod.).
Buccinofusus bernicicusis (King).
†‡§*Purpura lapillus* (L.).
**†Admete couthouyi*, Jay.
*†‡§*Eumargarita helicina* (Fabr.).
**†*E. grœnlandica* (Chem.).
Solariella cincta (Phil.).
**†Calliostoma occidentale* (Migh.).
†‡§*Lacuna crassior* (Mont.).
†*Littorina obtusata* (L.).[1]
†‡*L. rudis* (Mat.).
†*L. littorea* (L.).
†*Bela turricula* (Mont.).
†‡*B. trevelyana* (Turt.).
Typhlomangilia nivalis (Lov.).
Tornatina nitidula (Lov.).
†‡*Bullinella alba* (Brown).
†*Philine quadrata* (S. V. Wood).

* These species have seldom, if ever, been found south of the Wash.
† Also occurs in East North America.
‡ Also occurs in West North America.
§ Also occurs in Japan and Kamschatka.

The following members of the British molluscan fauna rank as 'southern species' (the list is not meant to be complete) :—

Lepidopleurus scabridus (Jeff.).
Acanthochites discrepans (Brown).
Barbatia lactea (L.).
Modiolus barbatus (L.).
Modiolaria costulata (Risso).
Crenella rhombea (Berk.).
Pteria hirundo (L.).
Pinna fragilis, Penn.
Loripes lacteus (L.).
Divaricella commutata (Phil.).
Diplodonta rotundata (Mont.).
Lepton squamosum (Mont.).
L. sulcatulum, Jeff.
Galeomma turtoni, Brod. & Sow.
Ervilia castanea (Mont.).
Tellina squalida, Pult.
T. donacina, L.
Donax variegatus (Gmel.).
Mactra glauca, Born.
Lutraria oblonga (Chem.).
Meretrix chione (L.).
Venus verrucosa, L.
Tapes decussatus (L.).
Cardium aculeatum, L.
C. tuberculatum, L.
Phasianella pullus (L.).
Littorina neritoides (L.).
Rissoa guerini, Récl., var. *costulata*, Ald.
Alvania cancellata (da Costa).
A. lactea (Mich.).
Ceratia proxima (Ald.).
Setia pulcherrima (Jeff.).
S. fulgida (J. Ad.).
Gallodina carinata (da Costa).
Adcorbis subcarinatus (Mont.).
Truncatella truncata (Mont.).
Calyptræa chinensis (L.).
Simnia patula (Penn.).
Erato lævis (Don.).

[1] North American, if *palliata*, Say, is to be regarded as a variety of *obtusata*, L.

Lunatia catena (da Costa).
L. sordida (Phil.).
Triforis perversa (L.).
Cerithiopsis tubercularis (Mont.).
Scala clathratula (Ad.).
Lotorium nodiferum (Lam.).
L. cutaceum (L.).
Cassidaria rugosa (L.).
C. echinophora (L.).
Cardium papillosum, Poli.
Solecurtus scopula (Turt.).
S. antiquatus (Pult.).
Barnea parva (Penn.).
Thracia pubescens (Pult.).
Dentalium vulgare, da Costa.
Emarginula conica, Schum.
Fissurella græca (L.).
Haliotis tuberculata, L.
Gibbula magus (L.).
G. umbilicata (Mont.).
Monodonta crassa (Montf.).
Calliostoma montagui (W. Wood).
C. exasperatum (Penn.).
C. striatum (L.).
C. granulatum (Born).
Donovania minima (Mont.).
Ocinebra erinaceus (L.).
O. corallina (Scac.).
Hædropleura ecostata (da Costa).
Mangilia attenuata (Mont.).
M. rugulosa (Phil.).
M. brachystoma (Phil.).
Bellardiella gracilis (Mont.).
Clathurella reticulata (Ren.).
C. purpurea (Mont.).
Haminæa hydatis (L.).
Philine catena (Mont.).
Aplysia depilans, L.
Pleurobranchus plumula (Mont.).
Oscanius membranaceus (Mont.).

The following species occur in the Channel Islands, but have not yet been met with in waters on the north side of the English Channel:—

? *Teredo pedicellata*, Quat.
Setia pulcherrima (Jeff.).
Haliotis tuberculata, L.
Lotorium nodiferum (L.).
L. cutaceum (L.).
Ocinebra corallina (Scac.).

Of the above, *L. nodiferum* has not again been found in British waters since three living specimens were trawled off Guernsey between 1825 and 1832. *L. cutaceus* is probably still an inhabitant, though rarely, of this station. I have myself picked up two worn shells at Herm, and Mr. Marshall dredged a living specimen off Guernsey, in 22 fathoms, in 1885.[1] *Purpura hæmastoma*, L., has probably not lived on these shores in recent years. There is a record [2] of the discovery of three specimens at Guernsey, but they were probably due to the refuse of French trawlers. Brest is the most northern authentic recorded habitat of the species.

P. Fischer remarks [3] that the English Channel "est une véritable barrière qui limite l'expansion vers le nord de 81 espèces de la côte française et de la Méditérranée". I do not feel quite clear whether Fischer meant that all the eighty-one species inhabit the southern coast of the English Channel. If they do not—and a consideration of the list makes it seem very unlikely that they do—the effectiveness of the 'véritable barrière' tends to disappear. Certainly, of forty-nine species which he cites specifically, six at least have been found on the northern side of the Channel since he wrote. A juster view of the case would appear to be, that not more of the Lusitanian fauna 'drop off' on the northern, as compared with the southern, side of the English Channel than one would naturally expect.

[1] Journ. Conch., vol. xiii, p. 202, 1911.
[2] J. T. Marshall, ibid., p. 197.
[3] Man. de Conch., 1887, p. 145.

The following species just reach the western coasts of the Channel and South and West Ireland:—

Lepidopleurus scabridus (Jeff.).
Acanthochites discrepans (Bronn).
Pteria hirundo (L.).
Crenella rhombea (Berk.).
Divaricella commutata (Phil.).
Lepton squamosum (Mont.).
L. sulcatulum, Jeff.
Galeomma turtoni, Brod. & Sow.
Cardium tuberculatum, L.
C. papillosum, Poli.
Thracia pubescens (Pult.).
Mactra glauca, Born.
Donax variegatus (Gmel.).
Emarginula conica, Schum.
Calliostoma exasperatum (Penn.).
C. striatum (L.).
Truncatella truncata (Mont.).
Calyptræa chinensis (L.).
Cassidaria tyrrhena (L.).
C. echinophora (L.).
Donovania minima (Mont.).
Mangilia rugulosa (Phil.).
Aplysia depilans, L.